

Joshua T. Ackerman · John McA. Eadie

## Current versus future reproduction: an experimental test of parental investment decisions using nest desertion by mallards (*Anas platyrhynchos*)

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**Abstract** Past investment in offspring may be important in determining a parent's ability to reproduce in the future and, hence, should affect the relative value of current offspring. However, there have been surprisingly few clear tests of whether animals actually adjust parental care in response to diminished opportunities for future reproduction. We modified the experimental protocol of Sargent and Gross [Behav Ecol Sociobiol (1985) 17:43–45] to examine offspring desertion by mallards (*Anas platyrhynchos*), and decoupled the influence of past investment from expected current benefits by controlling for the effect of offspring age on clutch value. Using 9 years of nest mortality data, we accounted for the increasing prospects of egg survival with clutch age by calculating clutch sizes throughout incubation with equivalent expected benefits. Applying this approach, we experimentally reduced 203 clutches at two different incubation stages such that they had equivalent expected benefits but differed in the amount of past investment. Nest desertion rates did not differ between early- and late-incubated clutches that had equivalent expected benefits. Rather, the probability of desertion increased with the severity of the clutch reduction treatment. These results suggest that female mallards adjust parental care according to the expected benefits of current offspring, rather than to diminished prospects for future reproduction due to past investment. We further examined whether females assessed expected benefits on the basis of clutch size alone or clutch size adjusted for the age of the clutch. Using Akaike's Information Criterion, the most parsimonious model to explain the probability of deserting an experimentally reduced clutch included both the proportion of the clutch remaining and clutch age. Thus, female mallards appear to fine-tune their level of parental care

not only according to the relative number of offspring in the clutch, but also to the increased prospects for offspring survival as they age.

**Keywords** *Anas platyrhynchos* · Clutch size · Nest desertion · Offspring age · Parental investment

### Introduction

Despite a long history of research in parental investment theory (Trivers 1972; Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977), there are still few clear tests of whether animals adjust their level of parental care in current offspring in response to diminished prospects for future reproduction (reviews by Sargent and Gross 1985; Curio 1987; Coleman and Gross 1991; Winkler 1991; Lavery 1995). Early studies focused predominantly on the question of whether animals commit the so-called Concorde fallacy, making parental care decisions so as not to "waste" investment accumulated to that point rather than providing care based only on the expected benefits of current offspring (Dawkins and Carlisle 1976; Weatherhead 1979; Dawkins and Brockman 1980). This issue generated much debate until it was resolved by simply incorporating life history theory into parental investment theory. Since reproduction is costly, past investment can reduce a parent's ability to reproduce in the future and, hence, will affect the relative value of current offspring (Williams 1966; Sargent and Gross 1985; Coleman and Gross 1991; Roff 1992; Stearns 1992). It is now widely accepted that parents might use past investment to determine the value of current offspring relative to future prospects for reproduction without acting fallaciously (Curio 1987; Coleman and Gross 1991).

Lost in the dust of the debate over the Concorde fallacy was the more interesting issue of the relative roles that past investment (i.e., diminished future reproductive prospects) and expected benefits from current offspring (i.e., current reproductive prospects) play in determining

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J. T. Ackerman (✉) · J. M. Eadie  
Department of Wildlife, Fish, and Conservation Biology,  
University of California,  
Davis, CA 95616, USA  
e-mail: jtackerman@ucdavis.edu  
Fax: +1-530-7524154

how animals adjust their level of parental care. Once it became clear that past investment in offspring might be important in determining a parent's ability to reproduce in the future (Sargent and Gross 1985; Coleman and Gross 1991), it seems that many researchers felt the debate was resolved and no longer of interest. Yet, it is still unclear whether, in practice, animals actually use their prior investment in offspring to make parental care decisions, and whether the use of past investment differs depending on a species' life-history and its breeding environment. For example, parental investment theory predicts that the influence of past investment on parental care decisions will depend on the predictability of environmental conditions; past investment becomes less important in unpredictable environments because reproductive success depends more on environmental conditions than on a parent's residual reproductive value (Coleman and Gross 1991).

Determining whether animals use their prior investment in offspring to adjust parental care is difficult and requires careful experimentation because expected benefits and past investment increase concomitantly with offspring age. Sargent and Gross (1985) proposed a novel experimental protocol to decouple past investment from expected benefits that used risk-taking behavior by parents in defense of offspring. While studies of offspring defense have been fruitful (review by Montgomerie and Weatherhead 1988), there may be a number of methodological problems in using defense behavior to assess parental care decisions (Knight and Temple 1986). Recently, studies have increasingly focused on offspring desertion to evaluate parental care behavior, especially in birds (review by Székely et al. 1996). Offspring desertion provides an unambiguous measure of parental investment since parents either stay with their offspring and continue to provide care, or they desert and terminate care before the offspring are capable of surviving independently (Fujioka 1989). Because parents derive no benefit from offspring they have deserted (but still could benefit from poorly defended young), analyses of offspring desertion may provide a more powerful test of parental investment theory than studies of nest defense behavior.

Using offspring desertion instead of nest defense to measure the level of parental care creates a unique challenge in decoupling the influence of past investment from the expected benefit of current offspring. The protocol of Sargent and Gross (1985) calls for reducing clutches to similar sizes, some during early incubation and others during late incubation, and then testing parental defense in all treatment groups shortly after manipulating clutches in the late-incubated treatment group. Thus, past investment has been altered because parents presumably expended more energy while incubating and caring for the larger clutch that was reduced late in incubation, whereas the expected benefits of current reproduction have been held constant because the number of eggs and their ages are similar when offspring defense is tested (e.g., Coleman et al. 1985; Winkler 1991). However, such an approach is not possible when

using offspring desertion because clutch reduction causes desertion (when it occurs) within 24 h (Armstrong and Robertson 1988; J.T. Ackerman, personal observations). Hence, the parental response (stay or desert) would be assessed at a younger age for the clutches reduced early in incubation than the clutches in the late-incubation treatment. Although past investment would still be larger in the late-incubated treatment group, the expected benefits also would be larger because the clutches would have aged and would be closer to hatching; past investment and expected benefits again would be coupled. Accordingly, studies using offspring desertion must devise an alternate method to manipulate past investment while controlling for expected benefits.

Here, we develop a modification of the experimental protocol of Sargent and Gross (1985) to use offspring desertion rather than nest defense to determine whether animals adjust parental care according to their level of prior investment in the current offspring, the expected benefits of the current offspring, or both. The expected benefit of current offspring increases with offspring age because the probability of survival for older offspring is greater than that for younger offspring (Montgomerie and Weatherhead 1988). We therefore decoupled past investment from offspring age by explicitly accounting for age-related influences on survival. Using long-term data on nesting mallards, *Anas platyrhynchos*, we calculated the probability of egg survival from the completion of clutch laying to hatching. We then used this probability of egg survival to calculate clutch sizes throughout the incubation period that had equivalent expected benefits. Applying this approach, we experimentally reduced mallard clutch sizes at different incubation stages (i.e., different clutch ages) such that they had equivalent expected benefits but differed in the amount of past investment, and we used nest desertion to measure the level of parental care. We also determined whether mallards adjust parental care according to the expected benefit of a current clutch by holding the stage of incubation (and past investment) constant while manipulating clutches to different sizes.

Nesting waterfowl are ideal for studying offspring desertion and the influence of past investment on parental care. Partial clutch loss by predators occurs frequently in ducks, and females often respond by deserting their remaining clutch (Ackerman 2002a). Female dabbling ducks such as mallards provide all parental care, so offspring desertion necessarily results in reproductive failure. Thus, it is likely that selection has acted strongly to shape parental behaviors in response to partial clutch loss. Furthermore, several studies have shown that waterfowl nesting in a variety of environments increase their parental care with incubation stage (Forbes et al. 1994; Sjöberg 1994; Mallory et al. 1998; Ackerman et al. 2003a), although it is unclear whether this relationship is due to the increasing expected benefits as clutches age or to the reduced prospects for future reproduction resulting from the investment of time and energy by females during incubation. In addition, waterfowl occupy a range of

breeding environments from the drought-susceptible Canadian prairie and pothole region, where recruitment is highly correlated with the number of ponds containing water (review by Johnson et al. 1992), to more stable boreal environments where there is less annual variation in wetland abundance (Nudds 1983; Bethke and Nudds 1993). Hence, waterfowl provide an excellent system in which to evaluate the influence of current versus future reproductive prospects on parental care decisions in variable breeding environments.

## Methods

### Study area and species

We conducted experiments in 1998 and 1999 at the Grizzly Island Wildlife Area in the Suisun Marsh of California (38°14' N, 121°97' W). As in the highly variable prairie environments of mid-continent North America (Krapu et al. 1983; Johnson et al. 1992), California has high annual variation in precipitation and is susceptible to drought, and mallard production appears to be related to spring precipitation (Mayhew 1955; McLandress et al. 1996). The Suisun Marsh is a large (~34,000 ha) brackish estuary at the downstream end of the Sacramento-San Joaquin Delta that drains into the San Francisco Bay. The Grizzly Island Wildlife Area contains approximately 2,000 ha of wetlands and 1,600 ha of upland habitats. Mallards are the most common dabbling duck (*Anatidae*, Tribe Anatini) nesting within these upland habitats (Ackerman 2002b). Female mallards lay one egg per day and begin the 26-day incubation period approximately when the full clutch is laid (about nine eggs; Klett et al. 1986; Afton and Paulus 1992). The young are precocial and leave the nest within 24 to 48 h of hatching; they are able to walk, swim, and feed on their own as soon as they leave the nest (Afton and Paulus 1992; Oring and Saylor 1992).

### Nest searching and monitoring techniques

Mallard nest search procedures were designed following Klett et al. (1986), modified by McLandress et al. (1996) for this study site. Nest searches were initiated in early April and continued until July to ensure finding both early- and late-nesting mallards (McLandress et al. 1996). Each area was searched four to five times at 3-week intervals until no new nests were found. Nest searches began at least 2 h after sunrise and were finished by 1400 hours to avoid missing nests due to morning and afternoon nest recesses by females (Caldwell and Cornwell 1975; Gloutney et al. 1993). Nest searches were conducted using a 50-m nylon rope strung between two slow-moving all-terrain vehicles. Tin cans containing stones to generate noise were attached at 1.5-m intervals along the length of the rope. The rope was dragged through the vegetation, causing females to flush from their nests and enabling observers to find nests by searching a restricted area. Each nest was marked with a 2-m bamboo stake placed 4 m north of the nest bowl and a shorter stake placed just south of the nest bowl, level with the vegetation height. Each nest was revisited on foot once every 7 days; the stage of embryo development was determined by candling (Weller 1956), and clutch size and nest fate (hatched, destroyed, or abandoned) were recorded. These data allowed us to determine which nests were appropriate for the study and the date on which we should experimentally manipulate each clutch.

### Model of equivalent expected benefits throughout incubation

We modeled the equivalent expected benefit of a clutch from the completion of laying to the last day of incubation. We used daily egg survival rates to calculate clutch sizes with equivalent expected

benefits for each day during the incubation period (i.e., clutch age). The daily probability of egg survival is a function of the daily Mayfield nest success rate (Mayfield 1961, 1975; Johnson 1979; Klett et al. 1986) and the daily probability that an egg will hatch in a successful nest (hereafter egg success, Sargeant and Raveling 1992). We assumed that the daily survival rates of nests and eggs were constant throughout the incubation period (see Miller and Johnson 1978). Using a long-term data set from our study site (California Waterfowl Association, unpublished data), we estimated daily egg survival rates according to the equation:

Daily egg survival

$$= (\text{Mayfield nest success}^{1/h}) \times (\text{egg success}^{1/h}), \quad (1)$$

where  $h$  is the mean age of clutches at hatching (Mayfield 1961, 1975; Johnson 1979; Klett et al. 1986), and Mayfield nest success and egg success estimates each were averaged (unweighted) over all 9 years. Because female mallards lay one egg per day and begin the incubation period (26 days) approximately when the full clutch (nine eggs) is laid, we set  $h$  equal to 35 days (Klett et al. 1986). Next, we calculated clutch sizes that had equivalent expected benefits at different stages in incubation according to the equation:

Equivalent clutch size<sub>at time  $i$</sub>

$$= (\text{original clutch size}) \times (\text{daily egg survival}^i), \quad (2)$$

where  $i$  equals the stage of incubation. Finally, because female mallards adjust their parental care after partial clutch loss according to the remaining clutch size relative to their original clutch size (i.e., the proportion of the clutch remaining), rather than the absolute remaining clutch size (Ackerman et al. 2003a), we converted the equivalent clutch size into the proportion of the original clutch (equivalent clutch size/original clutch size).

### Experimental clutch manipulations

Clutch-size manipulations were performed on either day 7±1 (early) or day 17±1 (late) of incubation. Therefore, females whose clutches were reduced late in incubation had invested in their clutch for an additional 10 days compared to females whose clutches were reduced early in incubation. We used only those nests that had not experienced a (natural) partial depredation event (e.g., Ackerman et al. 2003a, 2003b) prior to our experimental clutch manipulation. All clutch manipulations were performed by the same observer (J.T.A.) to avoid any confounding effects that different human intruders might have on parental response (Knight and Temple 1986).

Within the early and late groups, nests were systematically subjected to one of four treatments: small, medium, and large clutch reductions, and a control group in which clutches were disturbed (i.e., received similar nest visits and egg handling) but were not reduced experimentally. Early in incubation, we reduced clutches to 70%, 50%, and 30% of the original clutch size based on dabbling duck females' responses to naturally occurring partial clutch depredations (Ackerman et al. 2003a) and experimental clutch manipulations (Armstrong and Robertson 1988). For clutches reduced late in incubation, we used the model to determine the proportion of the clutch to remove for each treatment such that the expected benefits were equivalent to those in the early-incubation treatment groups (see Results; Fig. 2). Clutch-size manipulations were performed systematically throughout the nesting season to reduce temporal effects on parental care behavior, such as decreasing prospects for duckling survival (Orthmeyer and Ball 1990; Rotella and Ratti 1992; Dzus and Clark 1998) and decreasing potential for renesting (Montgomerie and Weatherhead 1988). After manipulating the size of a clutch, we covered the remaining eggs with nest materials (i.e., down and contour feathers from the nest), as the female would have done before leaving for an incubation recess.

We returned 2 days after each clutch manipulation to determine the female's decision to stay with or abandon the reduced clutch.



Since desertion generally occurs within 24 h of partial clutch loss (Armstrong and Robertson 1988; J.T. Ackerman, personal observations), a nest was considered to be active (i.e., not deserted) if we flushed the female from the nest subsequent to the clutch-size manipulation. If we did not flush the female from the nest 2 days after the clutch size manipulation, we used egg temperature, down placement, and embryonic development to determine whether the nest was deserted or the female was on an incubation recess (Klett et al. 1986). We returned to the nest the following day to confirm the nest's status (i.e., active or deserted). We excluded a nest from analyses if it was depredated after the clutch-size manipulation but before we could determine the female's decision to stay with or abandon the experimental clutch ( $n=29$ ), and we subjected the next available nest to the same treatment before continuing with the systematic treatment order. It is possible that these (excluded) nests actually had been deserted before they were depredated (e.g., nests may be more likely to be depredated after desertion), and that we are underestimating actual desertion rates by excluding these nests. However, this would not result in any systematic bias between early- and late-incubation treatment groups because a similar proportion of nests from each experimental group (13.9% and 10.2% of clutches manipulated in the early- and late-incubation treatment groups, respectively) were excluded.

### Statistical analysis

We detected no effect of year on females' decisions to stay with or abandon experimental treatments (hereafter clutch reduction treatment) either early (multiple logistic regression: Wald  $\chi^2 < 0.01$ ,  $n=124$ ,  $P=0.92$ ) or late in incubation (multiple logistic regression: Wald  $\chi^2=0.36$ ,  $n=79$ ,  $P=0.55$ ), or when the clutch reduction treatment and incubation stage were entered as main effects into the model (multiple logistic regression: Wald  $\chi^2=0.06$ ,  $n=142$ ,  $P=0.81$ ; control treatments excluded, see following discussion); we therefore pooled data from both years for analysis. To test whether females were more likely to desert treatment groups early in incubation rather than late in incubation (i.e., according to past investment), we used a multiple logistic regression model where the nominal dependent variable was stay or desert and the explanatory variables were the clutch reduction treatment (categorical factor: small, medium, or large clutch reduction), incubation stage (categorical factor: early or late), and an interaction term for clutch reduction treatment  $\times$  incubation stage. We excluded the control treatments from analyses of past investment because control treatment clutches in the early and late groups did not have equivalent expected benefits; control treatment clutches in the late group had a larger expected benefit than control treatment clutches in the early group due to offspring age. Control treatments were included in logistic regression analyses to test whether females invested according to the proportion of the clutch remaining (i.e., the expected benefit of a clutch; continuous variable). Unpaired  $t$  tests were used to compare female attributes (i.e., original clutch size laid and Julian nest initiation date) between early- and late-incubation treatment groups. All means are reported  $\pm 1$  SD.

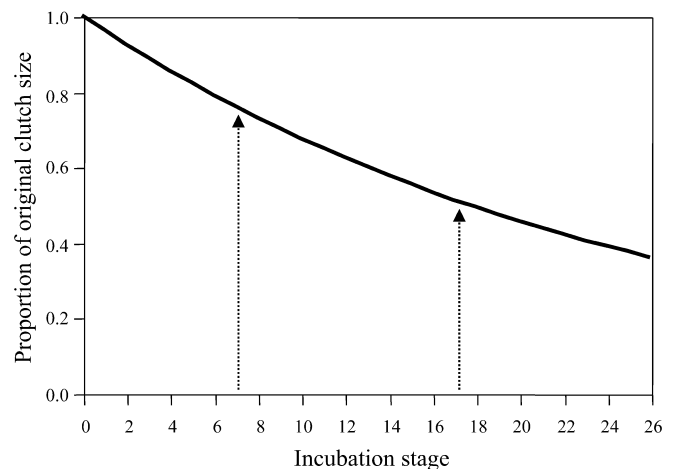
To determine whether females assessed expected benefits on the basis of clutch size alone (i.e., the proportion of the clutch remaining) or clutch size adjusted for age (i.e., the proportion of the clutch remaining weighted by incubation stage), we used Akaike's Information Criterion (AIC) to select the most parsimonious model for the probability of staying with an experimentally reduced clutch. For each model, we calculated log-likelihood values using multiple logistic regression. We used a second-order AIC for small sample sizes:  $AIC_c = -2(\log\text{-likelihood}) + 2K/(n-K-1)$ , where  $K$  is the number of fitted parameters and  $n$  is the sample size (Burnham and Anderson 1998; Anderson et al. 2000). We considered the model with the smallest AIC to be the most parsimonious (Burnham and Anderson 1998; Anderson et al. 2000). We calculated the  $AIC_c$  differences between the best model and the other candidate models ( $\Delta_i = AIC_{ci} - \text{minimum } AIC_c$ ) to determine the relative ranking of each model; models for which  $\Delta_i \leq 2$  have substantial support and were considered for biological importance

(Burnham and Anderson 1998; Anderson et al. 2000). Additionally, we calculated Akaike weights ( $w_i = \exp[-\Delta_i/2] / \sum \exp[-\Delta_i/2]$ ) to assess the weight of evidence that the selected model was the actual Kullback-Leibler best model in the set of models considered (Burnham and Anderson 1998; Anderson et al. 2000).

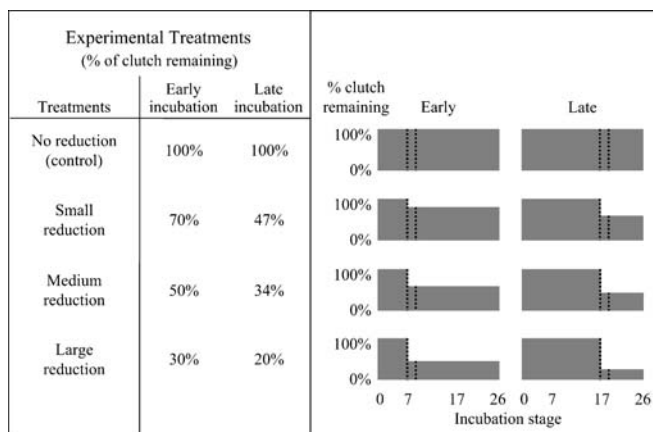
## Results

### Model of equivalent expected benefits throughout incubation

We calculated the daily egg survival rate using 9 years of data on mallards nesting within the Suisun Marsh (California Waterfowl Association, unpublished data). Between 1989 and 1997, 5,661 mallard nests were monitored (range: 315–902 nests per year). Among years, clutch size averaged 8.6 eggs (yearly range: 8.2–9.0 eggs). Mallard nest success averaged 30.3% (yearly range: 5.5–51.3%) and egg success averaged 83.2% (yearly range: 79.8–86.6%) resulting in an overall daily egg survival rate of 0.9614. Thus, a full clutch at the start of the incubation period had the equivalent expected benefit of a clutch with 36% (i.e.,  $1.0 \times 0.9614^{26}$ ) of the original clutch remaining just prior to hatching at 26 days in incubation (Fig. 1).



**Fig. 1** The expected benefit of current offspring increases with offspring age (i.e., incubation stage) because the probability of surviving to hatching for older offspring (eggs) is greater than that for younger offspring (eggs). We therefore decoupled past investment from offspring age by accounting for age-related influences on survival. We calculated the probability of egg survival from the completion of clutch laying to hatching using a 9-year data set on mallards at our study site (see Methods). Using these data, we modeled the equivalent expected benefit of a clutch from the completion of laying to the last (i.e., 26th) day of incubation. The solid line indicates the proportion of the original clutch size necessary for a female to have an equivalent expected benefit from current reproduction at each stage in incubation. For example, a full clutch at the start of the incubation period has the equivalent expected benefit of a clutch with 36% of the original clutch remaining just prior to hatching. We used this isocline of equivalent expected benefits to calculate experimental clutch reductions that had equal expected benefits between early- and late-incubated treatment groups (dashed arrows)

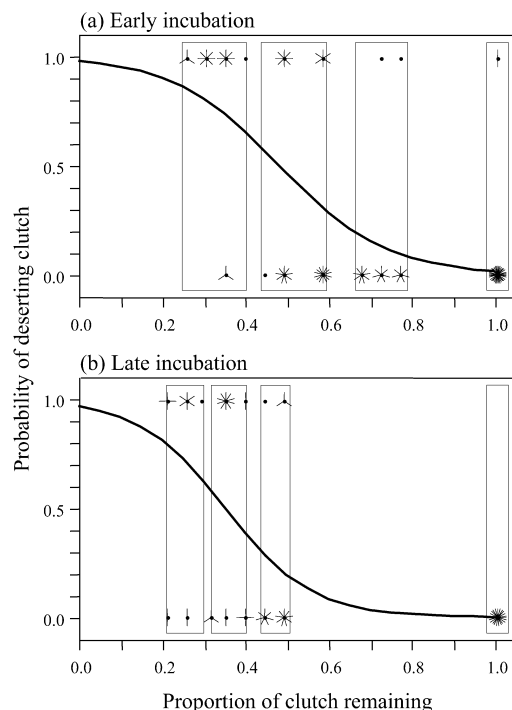


**Fig. 2** The experimental design. We experimentally reduced clutches on either the 7th (early incubation) or 17th (late incubation) day in incubation to one of three treatment levels with equivalent expected benefits; control clutches received similar nest visits and egg handling but were not reduced experimentally. *Dark shading* illustrates the proportion of the original clutch size remaining at the time of the experimental clutch manipulation and the hypothetical proportion of the original clutch remaining after the clutch manipulation if a predator did not depredate the nest subsequent to the manipulation. A female's parental investment decision (stay or desert) was measured 2 days after the experimental clutch manipulation. *Dashed lines* indicate the incubation stages when we experimentally manipulated clutches and when we assessed the female's parental investment decision. Mallards' incubation period is 26 days

We used this model to determine equivalent clutch sizes between early and late incubated treatment groups. The probability that an egg would survive the 10 days between the 7th and 17th day of incubation was 0.6746. Thus, the proportion of a clutch remaining after manipulation late in incubation had expected benefits equivalent to the proportion of the clutch remaining after manipulation early in incubation multiplied by 0.6746. For example, the expected benefit of a clutch reduced to 70% of its original size at 7 days in incubation was equal to that of a clutch reduced to 47% of its original size at 17 days in incubation (i.e.,  $0.70 \times 0.6746 = 0.47$ ; Fig. 2).

### Experimental clutch manipulations

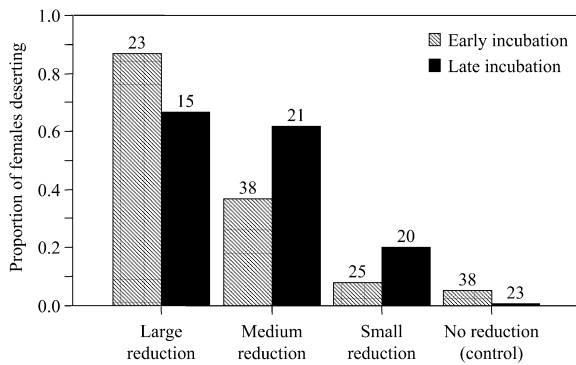
We experimentally manipulated 203 mallard clutches during 1998 and 1999; of these, 65 nests (32.0%) were deserted. High rates of nest depredation (overall nest success was 8.7% in 1998 and 8.2% in 1999) caused sample sizes to vary among treatments. We experimentally manipulated more clutches in the early-incubation treatment groups ( $n=124$ ) than in the late-incubation treatment groups ( $n=79$ ) simply because the clutches assigned to the late-incubation treatment groups were exposed for an additional 10 days and often had been depredated by the time they were to be manipulated (i.e., 17 days in incubation). We detected no differences between early- and late-incubation treatment groups in



**Fig. 3** The effect of experimental clutch reduction on nest desertion by female mallards during both (a) early incubation (logistic regression: likelihood ratio  $\chi^2=51.08$ ,  $n=124$ ,  $P<0.0001$ ) and (b) late incubation (logistic regression: likelihood ratio  $\chi^2=33.47$ ,  $n=79$ ,  $P<0.0001$ ). *Lines* indicate the logistic regressions between the proportion of the clutch remaining and the probability that a female would desert her remaining clutch. Equations are: **a**  $p(\text{desert})=1-[1/(1+\exp(3.76-7.79 \times \text{proportion of clutch remaining}))]$  and **b**  $p(\text{desert})=1-[1/(1+\exp(3.36-9.55 \times \text{proportion of clutch remaining}))]$ . *Boxes* indicate the data belonging to each treatment group; from left to right, the treatment groups are large reduction, medium reduction, small reduction, and control for each incubation stage. Each leg of a *star* indicates one data point

either the original clutch size that females laid ( $8.6 \pm 1.2$  eggs vs  $8.7 \pm 1.3$  eggs, respectively; unpaired  $t$  test:  $t=-0.25$ ,  $n_{\text{early}}=124$ ,  $n_{\text{late}}=79$ ,  $P=0.81$ ) or Julian nest initiation date ( $129.7 \pm 18.5$  days vs  $127.4 \pm 20.9$  days, respectively; unpaired  $t$  test:  $t=0.79$ ,  $n_{\text{early}}=124$ ,  $n_{\text{late}}=79$ ,  $P=0.43$ ). We obtained similar results when we excluded the control treatments from analyses. These results indicate that there were no systematic biases of female characteristics between early- and late-incubation treatment groups.

The probability of desertion decreased with the proportion of the clutch remaining, both during early incubation (logistic regression: likelihood ratio  $\chi^2=51.08$ ,  $n=124$ ,  $P<0.0001$ ) and late incubation (logistic regression: likelihood ratio  $\chi^2=33.47$ ,  $n=79$ ,  $P<0.0001$ ; Fig. 3). However, we found no difference in the probability of desertion between early- and late-incubated clutches that had similar expected benefits (control treatments excluded), nor was there a significant interaction between the clutch reduction treatment and incubation stage, whereas the effect of the clutch reduction treatment remained strong (multiple logistic regression: incubation stage:



**Fig. 4** The proportion of females deserting their remaining clutches in each treatment group, both early (shaded) and late (solid) in incubation. Control treatments were excluded from analyses testing whether females used their past investment in a clutch to make decisions about continuing parental care (see Methods). Numbers above bars indicate sample size

Wald  $\chi^2=0.51$ ,  $n=142$ ,  $P=0.48$ ; clutch reduction treatment  $\times$  incubation stage: Wald  $\chi^2=3.90$ ,  $n=142$ ,  $P=0.14$ ; clutch reduction treatment: Wald  $\chi^2=27.77$ ,  $n=142$ ,  $P<0.0001$ ; Fig. 4). When we dropped the interaction term from the analysis, there was still no detectable difference in the probability of desertion between early- and late-incubated clutches that had similar expected benefits (multiple logistic regression: incubation stage: Wald  $\chi^2=1.55$ ,  $n=142$ ,  $P=0.21$ ; clutch reduction treatment: Wald  $\chi^2=30.45$ ,  $n=142$ ,  $P<0.0001$ ). These results indicate that the probability of deserting an experimentally reduced clutch depended on the expected benefits of current reproduction and not on a female's past investment in the clutch.

According to our model (Fig. 1), the expected benefit of current reproduction should be a function of both the remaining clutch size and offspring age. By design, our experiment controlled for the increasing expected benefits as clutches age so that we could test for an effect of past investment on a female's decision to desert (Fig. 2). However, the decision to desert might be based only on the proportion of the clutch remaining (i.e., a static clutch-size threshold) and may not incorporate the increasing prospects for survival as clutches age during incubation. We tested this possibility directly using AIC model selection criteria. The most parsimonious model for the probability of staying with an experimentally reduced clutch contained both the proportion of the clutch remaining and clutch age (log-likelihood=-85.08,  $n=203$ ,  $K=3$ ,  $AIC_c=176.27$ ,  $\Delta_i=0.00$ ,  $w_i=0.91$ ), compared to candidate models that included only the proportion of the clutch remaining (log-likelihood=-88.44,  $n=203$ ,  $K=2$ ,  $AIC_c=180.93$ ,  $\Delta_i=4.66$ ,  $w_i=0.09$ ) or clutch age (log-likelihood=-127.15,  $n=203$ ,  $K=2$ ,  $AIC_c=258.35$ ,  $\Delta_i=82.08$ ,  $w_i=0.00$ ). Thus, female mallards do appear to adjust their level of parental care according to clutch size weighted by age; a result consistent with our model of equivalent expected benefits (Fig. 1).

## Discussion

Desertion of young is a common life-history strategy in a variety of taxa (e.g., Tait 1980; Robertson and Roitberg 1998; Jennions and Polakow 2001), and has recently become a central focus of investigations of parental care behavior in birds (review by Székely et al. 1996; Bauchau and Seinen 1997; Eadie and Lyon 1998; Hörak et al. 1999; Verboven and Tinbergen 2002; Ackerman et al. 2003a). Offspring desertion represents an unambiguous decision by parents and may provide a more powerful test of parental investment theory than nest defense behavior. Using offspring desertion as a measure of parental care also avoids many of the methodological problems in studies of avian nest defense. For example, model and live predators often do not elicit comparable behavioral responses from parents, and some seemingly defensive behaviors may not be appropriate indicators of parental care (Knight and Temple 1986). However, to use offspring desertion to test the role of past investment in adjusting parental care, existing methodologies need to be altered.

We modified the experimental protocol of Sargent and Gross (1985) by explicitly accounting for the effect that offspring age (via survival) has on the expected benefit of a clutch. With this approach, we were able to manipulate mallard clutch sizes at different stages in incubation such that they had equivalent expected benefits but differed in the amount of past investment by the parent (Fig. 2). We found no significant difference in the probability of desertion between early- and late-incubated clutches that had equivalent expected benefits (Fig. 4). Thus, female mallards did not use their prior investment in a clutch to make decisions about continuing their parental care.

We created the model of equivalent expected benefits throughout incubation (Fig. 1) using the unweighted average of 9 years of nest mortality data. However, females may be able to adjust their level of parental care according to the risk of nest depredation in a specific breeding year rather than the long-term average nest depredation risk. During the 2 years when the experimental clutch manipulations were performed, nest success was lower (1998:8.7%; 1999:8.2%) than the long-term average used to create the model (1989–1997:30.3%). Egg success during these 2 years (1998:78.0%; 1999:78.7%) was also lower than the long-term average (1989–1997:83.2%). Using the average values for these 2 years (instead of the long-term averages) would have resulted in a steeper decline in the equivalent expected benefit of a clutch (in Fig. 1) and would have resulted in even larger clutch reductions for each experimental treatment group late in incubation (in Fig. 2). Since the likelihood of nest desertion increases with the severity of clutch loss (this study; Armstrong and Robertson 1988; Ackerman et al. 2003a), desertion rates late in incubation would have been even higher (not lower) than those observed had we used clutch reductions based on nest depredation rates during the specific years of this study. Conversely, the past investment hypothesis predicts that desertion rates late in



incubation would be lower than those early in incubation. Therefore, the higher than normal nest depredation rates observed in 1998 and 1999 make our analysis more conservative, further supporting our conclusion that female mallards did not use their prior investment in a clutch to adjust their level of parental care.

Contrary to our results, the few other studies that have experimentally decoupled the influence of past investment from expected current benefits (*sensu* Sargent and Gross 1985) have found that prior investment in offspring has an important influence on the level of parental care (e.g., Coleman et al. 1985; Lavery and Keenleyside 1990). Possibly, our manipulation of past investment did not sufficiently alter the cost of reproduction. Although females whose clutches were reduced late in incubation had invested in their clutch for an additional 10 days compared to females whose clutches were reduced early in incubation, this additional amount of time and energy spent in incubation might not represent a significant cost in terms of an individual's life-time residual reproductive value. Thus, prior investment in offspring may have an influence on parental care decisions, but our manipulation of past investment may have been too small to detect its influence on the decision to desert. Despite the difficulty of detecting the costs of reproduction (Nur 1990), a variety of evidence suggests that the time and energy expended in incubation is a substantial cost. Female mallards lose 13% of their body mass during incubation (Krapu 1981; Gatti 1983), and 10 days represents 38% of the total time invested during incubation. Using Krapu's (1981) equation for mallard weight loss during incubation, females lost 6% of their body mass from the 7th to the 17th day of incubation. Therefore, when making the decision to desert an experimentally reduced clutch, females in the late incubation treatment groups probably were lighter than those in the early incubation treatment groups. Lower body mass of females at the end of a nesting attempt could reduce the probability of surviving to the next breeding season (e.g., wood ducks, *Aix sponsa*, Hepp et al. 1990), and lower the potential for future reproduction within the same breeding season since successfully nesting female mallards are significantly heavier than unsuccessful ones (Gloutney and Clark 1991). The additional 10 days spent in incubation also leaves less time remaining to renest during the current breeding season (Montgomerie and Weatherhead 1988), and breeding conditions deteriorate as the season progresses (Krapu et al. 1983; Eldridge and Krapu 1988). The time interval between successive breeding attempts in mallards is positively related to the number of days the eggs have been incubated (Swanson et al. 1986); hence, the extra 10 days spent in incubation likely delayed renesting. Altogether, the reproductive costs associated with the time and energy expended in the additional 10 days of incubation probably are substantial and should affect an individual's, life-time residual reproductive value.

Despite the time and energy costs associated with incubation, female mallards do not use their prior

investment in a clutch to adjust their level of parental care, possibly because it is a poor predictor of future reproductive success in this species. For many species of dabbling ducks, nests are subjected to intense predation (Cowardin et al. 1985; Klett et al. 1988; Greenwood et al. 1995) and unpredictable breeding environments (Krapu et al. 1983; Eldridge and Krapu 1988; Pietz et al. 2000; Gunness et al. 2001). In such situations, reproductive success depends largely on environmental conditions rather than a female's residual reproductive value (Coleman and Gross 1991). For example, predators are the primary cause of nest failure in mallards and limit recruitment substantially (review by Sargeant and Raveling 1992). Additionally, mallard production is strongly correlated with the number of ponds that contain water into the summer, a condition that is highly variable from year to year because many prairie wetlands are ephemeral (Johnson et al. 1992). Thus, past investment may not be a reliable predictor of future reproductive success in mallards. Rather, future reproductive success depends more on future breeding conditions, and the expected benefit of current reproduction should be a better indicator of clutch value relative to lifetime fitness for mallards and other dabbling ducks.

Indeed, the probability of desertion depended strongly on the proportion of the clutch remaining. Female mallards were more likely to desert clutches that experienced larger clutch reductions, both early and late in incubation (Fig. 3). Several previous studies of offspring desertion in waterfowl are consistent with our findings that desertion is related to attributes of the remaining clutch size. Eadie and Lyon (1998) showed that the probability of a female deserting experimentally reduced Barrow's goldeneye, *Bucephala islandica*, broods decreased with brood size. Pöysä et al. (1997) found that the time females spent caring for common goldeneye, *Bucephala clangula*, broods (before desertion) was negatively related to brood mortality rate (a measure reflecting both the number of young lost and the age of the brood). Armstrong and Robertson (1988) found that nest desertion rates for blue-winged teal, *Anas discors*, and northern shovelers, *Anas clypeata*, increased with the proportion of the clutch removed experimentally. Finally, in an observational study, we showed that the probability of nest desertion by mallard, gadwall, *Anas strepera*, and northern pintail, *Anas acuta*, females increased with the proportion of the clutch removed by predators during partial clutch depredation (Ackerman et al. 2003a). These data suggest that nest desertion in waterfowl is determined largely by attributes of the remaining clutch size (e.g., proportion of the clutch remaining).

Rather than a static clutch-size threshold, the response of mallards to clutch reduction appears to be finely tuned such that it incorporates the effect of offspring age (i.e., the probability of offspring survival) on the expected benefit of the clutch. Mallards were more likely to desert clutches reduced to similar sizes early in incubation than late (here, note that expected benefits differ due to offspring age; Fig. 3). For example, there was a 47%

chance that a female would desert a clutch reduced by half early in incubation compared to only a 20% chance late in incubation (Fig. 3). If mallards simply used a static clutch-size threshold, the probability of desertion would depend only on the proportion of the clutch remaining; however, if mallards adjust their level of parental care according to the expected benefit of current offspring, both the age of the clutch and the proportion of the clutch remaining should influence a female's response to clutch reduction (as in Fig. 1). We tested these alternatives directly using AIC model selection criteria (Burnham and Anderson 1998; Anderson et al. 2000), and found that the most parsimonious model to explain the probability of desertion contained both the proportion of the clutch remaining and clutch age. Thus, females adjusted their level of parental care according to clutch size weighted by age, a result that supports our model of equivalent expected benefits throughout incubation (Fig. 1). This finding has two important implications. First, it suggests that mallards are capable of fairly sophisticated adjustments in their level of parental care, including an ability to assess and respond to the expected survival of offspring according to their age. Second, it emphasizes the need to account for such effects in future studies of offspring desertion. If we had not developed an experimental design that allowed us to control for changes in expected benefits due to clutch age (Fig. 2), we may have concluded incorrectly that the increase in parental care with incubation stage was due to a female's past investment.

Several observational studies of waterfowl have reported an increase in parental care with incubation stage, but those studies could not determine whether this was due to an increase in offspring age per se or a female's past investment (Forbes et al. 1994; Sjöberg 1994; Mallory et al. 1998; Ackerman et al. 2003a). For example, the probability that female mallards would desert clutches that were reduced naturally by predators decreased with incubation stage (Ackerman et al. 2003a). After controlling for other variables known to influence parental care (e.g., proportion of the clutch remaining and eggshell remains), mallards were 1.14 times more likely to stay with a partially depredated clutch for each additional day spent in incubation (Ackerman et al. 2003a). The results of our present experimental study suggest that the increase in parental care with incubation stage observed in many waterfowl is a response to increasing expected current benefits as clutches age, rather than to diminished prospects for future reproduction due to the prior investment of time and energy expended by a female during incubation.

While the debate generated by the Concorde fallacy has long since subsided, an unfortunate consequence of that resolution is the impression that there may be little value in determining the influence of past investment on parental care decisions. On the contrary, both theoretical (Sargent and Gross 1985; Curio 1987; Coleman and Gross 1991) and empirical (Coleman et al. 1985; Lavery and Keenleyside 1990; Lavery 1995) studies demonstrate that past investment can shape parental care decisions by

devaluing future reproductive opportunities. Nonetheless, there are still remarkably few studies that have determined the role of past investment in parental care decisions while controlling for alternative explanations (sensu Sargent and Gross 1985). Renewed interest in the role of past investment could provide further insight into the pattern of increased parental care with offspring age observed in many species, and using analyses of offspring desertion (rather than defense) to test parental care decisions could provide more definitive conclusions. Understanding the importance of past investment in parental care decisions will also require research on how animals in variable environments, assess offspring value compared to those in more predictable breeding environments.

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